Palaearctic migrant waterbirds overlap in habitat use with residents at Lake Turkana, Kenya

M. Fasola, N. Saino, E. Waiyaki and O. Nasirwa

It is still uncertain whether the migrant birds that seasonally crowd African communities, use the same resources of, and compete with their analogue residents. Along a 56-km sector of the southeastern shores of Lake Turkana, northwestern Kenya, waterbird communities are exposed to conditions which may potentially provide a competitive context: in February, the densities of the resident and partial migrant waterbirds are similar to the July figures, while the migrants-mainly species capturing small invertebrate prey—are 20 times more abundant. The availability of small invertebrate prey in mud remains constant from February to July. Migrant birds overlap greatly in foraging habitat with residents. However, other results suggest that competition does not occur. The selection of specific foraging habitats seems due to physical constraints for most species. No species exhibited habitat shifts between February and July despite the densities of possible competitors having greatly changed. An exception is the Lesser Flamingo whose habitat shift cannot be attributed to competition. The rate of inter-species aggressions was very low. We conclude that at Lake Turkana, the arrival of Palaearctic migrant and partial migrant waterbirds does not induce competition with the residents, despite the strong increase in density, particularly of waders and of birds capturing small invertebrate prey.

Resource use within an assemblage of similar species may be constrained by competition between heterospecifics. Cautionary views have been expressed about the pervasiveness of competition. The partial segregation that is usually observed within animal assemblages may be due to factors other than competition, including intrinsic species preferences and opportunistic, non-interactive resource use (Connell 1980, Wiens 1989). Despite these cautions, some reviews of the available information showed that competition is pervasive in the assemblages of similar species, and is more pronounced in predators, large-sized organisms, and freshwater habitats (Schoener 1983, Connell 1983, Gurevitch 1992).

Bird communities in sub-Saharan Africa become somewhat crowded when Palaearctic migrant birds join the residents. One major but still unanswered question is whether the migrants compete with and use the same resources as their analogue African residents (Moreau 1972, Fry 1992). General observations and circumstantial evidence suggested that competition is much less than would have been expected (Moreau 1967, Morel 1973, Hogg *et al.* 1984). However, few quantitative studies have been conducted in tropical Africa on seasonal bird communities, on their resource use or on the possible competitive effects. The few studies (on passerines) showed that migrants are mainly insectivores, exploiting temporarily superabundant resources; that migrants exhibit infrequent aggressive interactions with residents; and that few cases of niche shifts have been observed in relation to the changes in migrant density and to the possible competitive pressure (Lack 1983, 1987, Rabøl 1987, Leisler 1992).

For waterbirds, no detailed community studies have been conducted in central Africa. Abundant data on waterbird populations have recently been collected (Perennou 1991), but only general descriptions of waterbird distribution within biotopes are available (for East Africa by Hogg *et al.* 1984, Brengballe *et al.* 1990).

The aim of our study was to compare the waterbird communities during the seasonal periods of peak and of low presence of Palaearctic migrants along a representative sector of shoreline at Lake Turkana. We describe the changes in community structure, analyse the use of foraging habitat by Palaearctic migrant, partial migrant, and resident waterbirds, and seek indications of possible competitive interactions between residents and migrants.

Study area and methods

We surveyed a 56-km sector of the southeastern shore of Lake Turkana, which is the largest of the Kenyan Rift Valley lakes. This shore sector stretches from 13 km south of Loyengalani to Soiti $(2^{\circ}41-3^{\circ}02N, 36^{\circ}26-36^{\circ}40E)$. The shore has major representative habitat types of Lake Turkana in relatively similar proportions. It has 13.0 km of mudflats, 15.7 km of sandy shores, 14.3 km of pebbles and 13.0 km of rocky shores. However, the large reedbeds and mudflats of the Omo Delta at the northern side are under-represented in our sector. Two surveys were conducted on this shore sector, one from 25 January to 22 February 1992 prior to the breeding season of residents and immediately prior to the beginning of the northward movement of Palaearctic migrants, and the second survey from 8 to 14 July 1993 after the residents' breeding season and when migrant presence is minimal (Brown *et al.* 1982). The species, their scientific names and their migrant or resident status are listed in Table 1.

During morning surveys we covered the entire shore sector and we censused all the waterbirds, regardless of their foraging or resting activities. This does not bias the census results because the waterbirds remained in the same area for resting and foraging throughout all the 24-h period (Fasola & Canova 1993).

Waterbird habitat use was recorded in the three large muddy bays, Loyengalani, El Molo and Sandy Bay, where waterbird abundance and species richness were highest (Fasola *et al.* 1993a). We recorded the habitat of each waterbird that was foraging when spotted, while we walked along the shore, stopping every 100 m in order to scan all the waterbirds. An unbiased sample of all species was obtained, as waterbirds at Lake Turkana forage within a narrow strip along the shoreline, approximately 100 m in water and 50 m on land. Initially we observed all the individuals encountered, but during the last days of each survey we concentrated our records on those species for which we had less than 200 records. We recorded 13 444 foraging locations in February and 2306 in July. Foraging habitat was categorized into six categories: deep water (where birds swam); shallow water (where birds walked with water above their feet); water's edge (the narrow borderline between water and land); wet mud; dry mud (bare) and grass (soil covered by sparse and short grass in the few wet patches bordering dry mud). For birds in shallow water we estimated the proportion of their

Table 1. Waterbirds densities along the southeastern shores of Lake Turkana.
Species status: M = Palaearctic migrants, breeding in the Palaearctic and spending the northern winter in the Turkana area; P = partial migrants with some populations breeding in equatorial Africa, or migrants within central Africa;
R = residents, breeding in equatorial Africa. Species' prevailing food, categorized as: L = captures large prey; G = grazes plant and animal materials; F = filters small particles; S = pecks small prey. Status and food categories from Brown et al. (1982), and Urban et al. (1986)

			density (birds km ⁻¹)	
	status	food	Feb	Jul
Little Grebe Tachybaptus ruficollis	R	L	3.7	1.0
Great Cormorant Phalacrocorax carbo		L	6.1	9.8
Long-tailed Cormorant Phalacrocorax africanus		L	7.5	3.4
African Darter Anhinga rufa	R	L	0.02	
Great White Pelican Pelecanus onocrotalus	R	L	0.3	0.7
Pink-backed Pelican Pelecanus rufescens		L	1.8	2.1
Cattle Egret Bubulcus ibis	MPR	S	0.4	0.02
Black Heron Egretta ardesiaca	MR	L		0.04
Western Reef Egret Egretta gularis	Р	L	0.03	
Little Egret Egretta garzetta	MR	L	2.8	2.7
Great White Egret Casmerodius albus	MR	L	0.1	
Grey Heron Ardea cinerea	MR	L	0.9	0.7
Black-headed Heron Ardea melanocephala	R	L		0.1
Goliath Heron Ardea goliath	R	L	0.1	0.1
Yellow-billed Stork Mycteria ibis	R	L	0.4	1.4
Glossy Ibis Plegadis falcinellus	MR	S	1.5	1.4
Sacred Ibis Threskiornis aethiopicus	R	S	1.2	1.0
African Spoonbill Platalea alba	MPR	L	2.0	1.0
Greater Flamingo Phoenicopterus ruber	MR	F	8.5	0.6
Lesser Flamingo Phoeniconaias minor	R	F	3.1	33.3
Osprey Pandion haliaetus		L	0.4	0.02
African Fish-eagle Haliaeetus vocifer	R	L	0.1	0.1
Eurasian Marsh-harrier Circus aeruginosus	М	L	0.02	
White-faced Whistling-duck Dendrocygna viduata	R	G	3.2	0.1
Egyptian Goose Alopochen aegyptiacus	R	G	16.1	11.0
Knob-billed Duck Sarkidiornis melanotos	MPR	G	0.02	
Eurasian Wigeon Anas penelope	М	F	0.9	
Northern Pintail Anas acuta	M	F	2.5	
Hottentot Teal Anas hottentota	R	F	0.5	
Northern Shoveler Anas clypeata	M	F	0.9	

				nsity s km ⁻¹)
	status	food	Feb	Jul
Southern Pochard Netta erythrophthalma	MPR	F		0.05
Red-knobbed Coot Fulica cristata	R	G	1.8	0.3
Common Stilt Himantopus himantopus	MR	S	1.6	0.1
Eurasian Avocet Recurvirostra avosetta	MR	S	0.4	0.02
Senegal Thicknee Burhinus senegalensis	R	S	0.7	0.6
Common Pratincole Glareola pratincola	MR	S	4.1	3.0
Spur-winged Lapwing Vanellus spinosus	R	S	9.9	8.8
Gray Plover Pluvialis squatarola	Μ	S	0.1	
Ringed Plover Charadrius hiaticula	Μ	S	19.3	
Little Ringed Plover Charadrius dubius	Μ	S	0.1	
Kittlitz's Sandplover Charadrius pecuarius	R	S	11.3	3.2
Three-banded Plover Charadrius tricollaris	R	S	0.02	
Kentish Plover Charadrius alexandrinus	М	S	0.02	
Greater Sandplover Charadrius leschenaultii	Μ	S	0.02	
Caspian Plover Charadrius asiaticus	Μ	S	0.6	
Eurasian Curlew Numenius arquata	М	S	0.03	
Black-tailed Godwit Limosa limosa	Μ	S	5.6	0.05
Spotted Redshank Tringa erythropus	Μ	S	0.02	
Redshank Tringa totanus	М	S	0.2	0.02
Greenshank Tringa nebularia	М	S	4.1	0.2
Marsh Sandpiper Tringa stagnatilis	М	S	4.1	
Wood Sandpiper Tringa glareola	М	S	1.8	0.04
Common Sandpiper Actitis hypoleucos	Μ	S	5.9	0.05
Ruddy Turnstone Arenaria interpres	М	S	0.8	
Little Stint Calidris minuta	М	S	168.3	
Curlew Sandpiper Calidris ferruginea	М	S	8.8	
Ruff Philomachus pugnax	М	S	3.2	
Grey-headed Gull Larus cirrocephalus	R	L	13.1	21.6
Black-headed Gull Larus ridibundus	Μ	L	4.7	0.2
Lesser Black-backed Gull Larus fuscus	М	L	3.04	0.8
Gull-billed Tern Sterna nilotica	М	L	1.4	0.05
Caspian Tern Sterna caspia	MR	L	0.4	
Little Tern Sterna albifrons	М	L	0.3	
Whiskered Tern Chlidonias hybridus	MR	L	0.2	
White-winged Black Tern Chlidonias leucopterus	М	L	3.6	
African Skimmer Rynchops flavirostris	R	L	1.3	0.3

legs that were submerged, and afterwards we calculated water depths from data on average tarsus length (Brown *et al.* 1982, Urban *et al.* 1986). During data analysis, depths were classed as <2, 2-4, 4-8, 8-16, 16-32, and >32 cm. We also recorded any aggressive interaction among the waterbirds during the first scan of their activity.

The availability of invertebrate aquatic prey was found by: collecting cylindrical samples of mud with 11 cm diameter by 20 cm depth (92 samples in February and 66 in July), sieving the material through a 1-mm mesh, storing the organic material in formalin, and identifying the invertebrates under a dissection microscope. Mud samples were collected at an equal number of sites in water, lake edge, and wet mud.

A species' distribution among habitat categories was compared with that of another species, or with that of the same species in a different period, by χ^2 tests based on the location frequencies of each species. Since behaviour within a flock is not independent among individuals, the tests were conservative, being based on the frequencies of flocks (conspecific birds observed from one spot and foraging in the same habitat category) and not on the frequencies of individual birds.

Results

Seasonal communities

We recorded 66 waterbird species (Table 1), a large subset of those found during more extensive surveys of lake Turkana by Hopson & Hopson, 1975 (120 species), by Schekkerman & van Wetten, 1987 (83 species) and by Bennun & Fasola, in press (107 species). The species recorded by others but not but not by us are those tied to habitats absent from our area, e.g. reed beds, or species of sporadic occurrence.

Residents or partial migrants maintained similar densities in July and February (Table 1). Most Palaearctic migrant species were completely absent in July, with only Greenshanks, Black-headed and Lesser Black-backed Gulls present in notable numbers.

In February, the Palaearctic migrants dominated (69 per cent of the birds) the waterbird community (Table 2), whereas in July the community was composed almost exclusively of residents (60 per cent) and partial migrants (36 per cent). The overall waterbird density in July was only one third of that in February. The low July densities were mainly due to the decrease of the Recurvirostridae, Charadriidae, Scolopacidae and Anatidae, and of species which feed by pecking small prey. The other families—and the species which feed by capturing large prey, by grazing and by filtering—maintained similar densities (Table 2).

Habitat use

Species were unevenly distributed on the four types of shore category. Most species had their highest densities on muddy shores and pebbles, many used sand (though to a lower degree), and a few preferred rocks, as already described by Fasola *et al.* (1993b). In this paper we only describe habitat use only on muddy shores because it had the

	Density (birds/km)		
	February	July	
Residents	77.0	65.3	
Partial migrants	29.9	39.0	
Palaearctic migrants	239.7	4.6	
Anatidae	25.8	11.4	
Ciconiiformes	9.1	7.4	
Accipitridae	0.7	0.2	
Laridae, Sternidae	31.6	25.9	
Podicipedidae, Phalacrocoracidae, Anhingidae, Pelecanidae	18.8	17.0	
Phoenicopteridae	19.9	33.9	
Recurvirostridae, Burhinidae, Charadriidae, Scolopacidae	240.7	13.1	
Captures large prey	53.5	46.0	
Grazes	21.1	11.4	
Filters	24.7	34.0	
Pecks small prey	247.5	17.5	

Table 2. Seasonal composition of the waterbird community of Lake Turkana

 Table 3. Frequency of aggressions (percentage of birds scanned that were engaged in aggressions) recorded in February

Aggressor	Aggressed (- for conspecifics)	
African Spoonbill		0.23
Ringed Plover	-	0.27
Ringed Plover	Kittlitz's Plover	0.80
Kittlitz's Plover		0.29
Little Stint		0.08
Black-tailed Godwit	-	0.08
Ruff	Curlew Sandpiper	0.45
Greenshank		0.38

highest species richness and bird abundance, and because it reflects a consistent zonation from the open water to the dry land.

We describe habitat use for the 26 dominant species only, and omit the species which had fewer than six individuals in our study area; that mostly foraged away from the strip of shoreline that could be effectively surveyed (Little Grebe, Cattle Egret, Common Pratincole, all the Laridae and Sternidae); that foraged almost entirely in deep water (Great Cormorant, Long-tailed Cormorant, Great White and Pink-backed Pelicans, Northern Pintail, Northern Shoveler and Red-knobbed Coot); and those that were almost entirely restricted to rocks and pebbles (Senegal Thicknee, Redshank, Ruddy Turnstone).

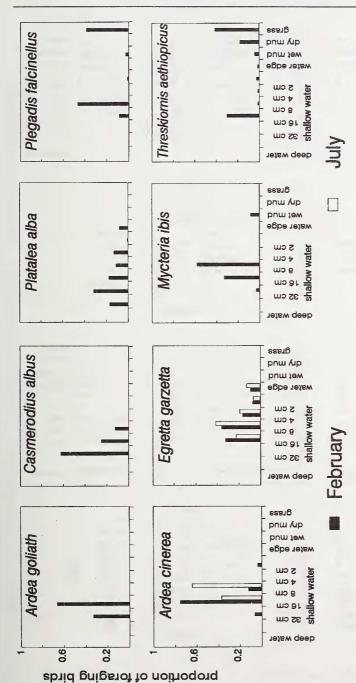
Figures 1, 2 and 3 show foraging habitat use on muddy shores by the 26 waterbird species. Grouping of species in these figures in pairs (e.g., Grey and Goliath herons in Fig. 1) or trios (e.g., Egyptian Goose, White-faced Whistling Duck and Hottentot Teal in Fig. 3) is based on similarity in taxonomy and size.

Despite a partial overlap in foraging habitat by the members of these similar pairs or trios, each species used habitats that differed significantly from those used by similar species (the frequency distributions of each species pair were all significantly different when submitted to χ^2 tests), during both February and July. In many cases, habitat use simply reflected the capacity of the larger species to wade in deeper waters than the smaller ones (Goliath Heron v Grey Heron, Great White Egret v Little Egret, Avocet v Black-winged Stilt, Greenshank v Marsh Sandpiper). In other cases, habitat differences seem not to reflect merely size differences. Lesser Flamingos foraged mostly in very shallow waters or even on wet mud, and were clearly segregated from Greater Flamingos. Kittlitz's Plovers were more terrestrial than the very similar Ringed Plovers, while Ruffs were sharply segregated from Black-tailed Godwits and Common Sandpipers from Wood Sandpipers.

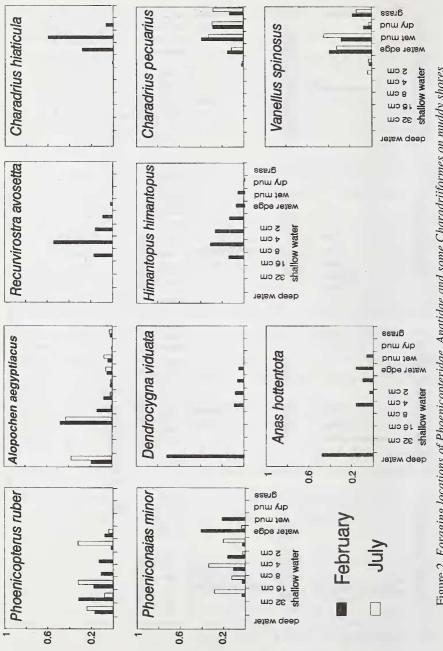
During July, data on habitat use were available for only seven species (Figs. 1, 2, 3), and we could only test seasonal differences in habitat use on these seven. Only Lesser Flamingos showed a significant shift towards deeper waters in July than in February ($\chi^2 = 27.3$, d.f. = 6, P < 0.01). The other six species foraged in the same habitat categories as in February (the χ^2 tests on the location frequencies of the same species in February and in July were not significant).

Prey availability was similar, and very low, in both February and July. Prey densities in the two periods were 8.3 and 9.6 items m^{-2} , respectively. Prey composition in mud comprised insect larvae and worms, ranging in size 4–7 mm in length and 1–3 mm in diameter.

Inter- or intra-specific aggressions were observed only in February, and at very low frequencies (Table 3). African Spoonbills, Ringed Plovers, Kittlitz's Plovers, Little Stints, Black-tailed Godwits and Greenshanks performed interspecific aggressions, but only for less than 0.5 per cent of the individuals scanned. The only interspecific aggression was seen in Ringed Plovers which displaced Kittlitz's Plovers (0.8 per cent of individual Ringed Plovers scanned), and in Ruffs which displaced Curlew Sandpipers (0.5 per cent of Ruffs scanned).







proportion of foraging birds

Figure 2. Foraging locations of Phoenicopteridae, Anatidae and some Charadriiformes on muddy shores

28



Figure 3. Foraging locations of some Charadriiformes on muddy shores

Discussion

Habitat use by foraging waterbirds may be determined by their feeding behaviours and by physical constraints: for example, with divers preferring deep water. Species that feed by wading are constrained to depths dictated by the length of their tarsi. Competition—the common use of a limiting resource by consumer species—may further restrict habitat uses as it is determined by behaviour and physical constraints. However, habitat segregation provides only weak evidence of competition and even if niches were arranged randomly, differences would still exist (Wiens 1989). Two types of competitive interactions are commonly recognized: exploitation (diminished resource availability because of use by other species), and interference (aggression limiting access to resources). Aggressive interference between migrants and residents seems to be infrequent (Leisler, 1992), but it was documented for landbirds in West Africa (Edington & Edington, 1983) and for ducks overwintering in the temperate Nearctic (Alexander, 1987). Habitat is the resource which most frequently segregates bird species within guilds (Wiens 1989), and migrants and residents under competitive pressure can be expected to display habitat partitioning.

Our results, and particularly the following points, suggest that waterbird communities at Lake Turkana are exposed to conditions which may potentially provide a competitive context.

- The densities of resident and partial migrant waterbirds are similar in February and in July, while those of Palaearctic migrants are 20 times higher in February than in July, thus producing a sharp increase in the abundance of possible competitors. The increase was mainly due to the arrival of species that feed on small invertebrate prey.
- The availability of small invertebrate prey in mud seems to remain constant in February and in July, contrasting with temperate latitudes, where the densities of intertidal invertebrates fluctuate markedly between seasons (Puttick 1984). It is surprising that prey densities in our samples were lower by two orders of magnitude than in the samples collected by similar methods in temperate latitudes (Meire & Kuyken 1984, Szekely & Bamberger 1992).
- Migrants overlapped greatly in use of foraging habitats with residents. This
 overlap was particularly high for small waders and for Ciconiiformes; the migrant
 Anatidae, on the other hand, were partially segregated from resident geese and
 ducks.

However, the following other results indicate that competition is not relevant.

- The segregation of most species into specific foraging habitats seems not to result from competition but from physical constraints of tarsus length. There are only a few species pairs where the partial segregation in foraging habitat suggests some interspecific competitive interaction: Kittlitz's v Ringed Plovers (resident v migrant); Ruffs v Black-tailed Godwits and Common v Wood Sandpipers (migrant v migrant). No habitat shifts occurred between February and July despite the densities of possible competitors having greatly changed. The only case of habitat shift occurred in Lesser Flamingos during July, when their densities were higher than in February and the densities of Greater Flamingos lower. Lesser Flamingos seem to be displaced spatially when Grater Flamingos abound, although it is practically impossible that these two flamingos compete for food, given their totally different food requirements (Brown et al. 1982).

The frequency of inter-species aggressions was very low, and were recorded only between Ringed and Kittlitz's Plovers, and Ruffs and Curlew Sandpipers. However, Kittlitz's Plovers did not shift their foraging habitat in July, when the other plovers were absent, therefore they do not seem to compete with the other plovers, despite their partial habitat segregation and the occurrence of aggressions.

We conclude that at Lake Turkana, the arrival of Palaearctic migrant and partial migrant waterbirds does not induce competition with the residents, despite the strong increase in density, particularly of waders and species capturing small invertebrate prey.

No other information exists on habitat use and competition by waterbirds in Central Africa. In the Neotropics, Duffy *et al.* (1981) found no evidence that inter-species competition affects the distribution of wintering shorebirds. On the other hand, for temperate Europe there is evidence that during winter, waders may deplete their food supplies and suffer high mortalities (Evans *et al.* 1984). Similarly to our results, there are indications that the potential competition between Palaearctic migrant landbirds and their Afrotropical resident analogues is less than might be expected (Morel 1973, Hogg *et al.* 1984, Leisler 1992).

Acknowledgements

The expeditions to Lake Turkana were financed by a grant AI93.00112.04 from the Comitato Nazionale Ricerche and by contributions from the Cassa Risparmio delle Province Lombarde (Pavia). Others who provided support were the Instituto Nazionale Fauna Selvatica (Bologna, Italy), Zeiss (Milano), Ferrino (Torino), Olivetti Equatorial Ltd and Sogei Ltd (Kenya). Technical support was provided by the Ornithology Department of the National Museums of Kenya for which we are most grateful. We also wish to thank the participants, and in particular, L. Bennun, L. Biddau, L. Borghesio and L. Canova, for the part they played in the expeditions.

References

- ALEXANDER, W.C. 1987. Aggressive behaviour of wintering diving ducks (Aythini). Wilson Bulletin 99: 38-49.
- BENNUN, L. & FASOLA, M. (in press) Resident and migrant waterbirds at Lake Turkana, February 1992. Quaderni Civica Stazione Idrobiologica Milano.
- BRENGBALLE, T., HALBERG, K., HANSEN, L.N., PETERSEN, I.K. & THORUP, O. 1990. Ornithological winter survey on the coasts of Tanzania 1988–89. Research Report 43. International Council Bird Preservation, Danish Section: Copenhagen.

- BROWN, L.H., URBAN, E.K. & NEWMAN, K. 1982. The birds of Africa. Vol. 1. London: Academic Press.
- Connell, J. H. 1980. Diversity and coevolution of competitors, or the ghost of competition past. *Oikos* 35: 131–138.
- CONNELL, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122: 661–696.
- DUFFY, D.C., ATKINS, N. & SCHNEIDER, D.C. 1981. Do shorebirds compete on their wintering grounds? Auk 98: 215–229.
- EDINGTON, J.M. & EDINGTON, M.A. 1983. Habitat partitioning and antagonistic behaviour amongst the birds of a West African scrub and plantation plot. *Ibis* 125: 74–89.
- EVANS, P.R., GOSS-CUSTARD, J.D. & HALE, W.G. (EDS) 1984. Coastal waders and wildfowl in winter. Cambridge: Cambridge University Press.
- FASOLA, M., BIDDAU, L., BORGHESIO, L., BACCETTI N. & SPINA, F. 1993a. Water birds populations at Lake Turkana, February 1992. Proceedings of the VIII Pan-African Ornithological Congress: 529–532.
- FASOLA, M., BIDDAU, L. & BORGHESIO, L. 1993b. Habitat preferences of resident and Palaearctic water birds at lake Turkana. *Proceedings of the VIII Pan-African Ornithological Congress*: 539–545.
- FASOLA, M., & CANOVA, L. 1993. Diel activity of resident and immigrant waterbirds at Lake Turkana, Kenya. *Ibis* 135: 442–450.
- FRY, C.H., BRITTON, P.L. & HORNE, J.F.M., 1974. Lake Rudolf and the Palaearctic exodus from East Africa. *Ibis* 116: 44–51.
- GUREVITCH, J., MORROW, L. L., WALLACE, A. & WALSH, J. S. 1992. A meta-analysis of competition in field experiments. *American Naturalist* 140: 539–572.
- HOGG, P., DARE, P.J. & RINTOUL, J.V. 1984. Palaearctic migrants in the central Sudan. *Ibis* 126: 307–331.
- HOPSON A.J. & HOPSON, J. 1975. Preliminary notes on the birds of the Lake Turkana area. Kitale: cyclostyled.
- LEISLER, B. 1992. Habitat selection and coexistence of migrants and Afrotropical residents. *Ibis* 134 Supplement 1: 77–82.
- MEIRE, P. & KUYKEN, E. 1984. Relations between the distribution of waders and the intertidal benthic fauna of the Oosterschelde, Netherlands. pp 56–68 in: Evans, P.R., Goss-Custard, J.D., Hale, W.G. Coastal waders and wildfowl in winter. Cambridge: Cambridge University Press.
- MOREAU, R.E. 1967. Water birds over the Sahara. Ibis 109: 232-259.
- MOREAU, R.E. 1972. The Palaearctic-African bird migration systems. London: Academic Press.
- MOREL, G. 1973. The Sahel zone as an environment for Palaearctic migrants. *Ibis* 115: 413–417.
- PERENNOU, C. 1991. Les recensements internationaux d'oiseaux d'eau en Afrique tropicale. International Waterfowl and Wetlands Research Bureau Special Publication no. 15. Slimbridge: IWRB.
- PUTTICK, G.M. 1984. Foraging and activity patterns in wintering shorebirds. pp. 203–231 in BURGER, J. & OLLA, B.L. Shorebirds. Migration and foraging behavior. New York: Plenum Press.
- SCHEKKERMAN, H. & Van WETTEN, J.C.J. 1987. An ornithological survey of Lake Turkana, Kenya. Dutch Working Group International Wader Waterfowl Research Report 17: 54.

- SCHOENER, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* 122: 240–285.
- SZEKELY, T. & BAMBERGER, Z. 1992. Predation of waders (Charadrii) on prey populations: an enclosure experiment. *Journal of Animal Ecology* 61: 447–456.

URBAN, E.K., FRY, C.H. & KEITH, S. 1986. The birds of Africa. Vol. 2. London: Academic Press.

WIENS, J. A. 1989. *The ecology of bird communities*. Vol. 1. Cambridge: Cambridge University Press.

M. Fasola, Dipartimento Biologia Animale, Università di Pavia, Piazza Botta 9, Pavia, Italy, N. Saino, Dipartimento Biologia, Via Celoria, Milano, Italy, E. Waiyaki and O. Nasirwa, National Museums of Kenya, Box 40658, Nairobi, Kenya

Scopus 18: 20-33, November 1994

Received 25 May 1994

Notice

